Fallen into oblivion—the systematic affinities of the enigmatic *Sulcospira* Troschel, 1858 (Cerithioidea: Pachychilidae), a genus of viviparous freshwater gastropods from Java

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ABSTRACT

Sulcospira Troschel, 1858, is not only the taxonomically oldest but also one of the most poorly known genera of Southeast Asian Pachychilidae. It serves as an instructive case study as to how the puzzling systematics of freshwater Cerithioidea has hampered a deeper understanding of their phylogeny and evolution. The genus has been established for the Javan freshwater gastropod *Melania sulcospira* Mousson, 1849, on the grounds of its round, multispiral operculum and an elongated main cusp in the central radula teeth. Although of great systematic significance, this taxon has been widely ignored by subsequent authors. We here recapitulate the taxonomic history of the genus and describe and evaluate the morphological properties of the type species *S. sulcospira* on basis of the limited existing material, in order to facilitate a better understanding of pachychilid systematics. In addition, in an attempt to clarify its systematic affinity, we compare the properties of another allegedly related species from Java, *S. martini* (Schepmann, 1898). We show that these two viviparous species exhibit different protoconch morphologies, which are indicative of reproductive strategies distinct from other pachychilids. Finally, we outline preliminary suggestions as to the systematics of *Sulcospira* within the family Pachychilidae.

MATERIALS AND METHODS

Materials

This study is based on the examination of material from various museum collections worldwide (see repositories). All of these samples comprise dry shells only, which as a rule were empty. Only few shells contained fragmentary soft parts; some of them were re-hydrated for examinations. However, these bodies generally did not facilitate morphological examinations except for the extraction of small radula fragments. We have not tried to extract DNA from dried tissues because earlier attempts with comparable material of *Brotia* failed. In order to acquire fresh material, collecting trips have been undertaken in 2000 and 2002. We have searched rivers and creeks in different sectors of there course (i.e. upstream, midstream, downstream) for a period of altogether 7 days in West Java (along the roads between Jakarta and Serang, Bogor and Sukabumi, Sukabumi and Pelabuhan Ratu, Bogor and Cipanas, Bogor and Cianjur, in the Botanical Garden Bogor) and for 3 days in East Java (between Taksimalaya, Cipatujah, and Pangadaran). During these trips we were not able to find any material of *Sulcospira*, though.

Because freshwater biotopes on Java are facing dramatic devastation by a multitude of causes related to the dense population on this island such as pollution, flow regulation, drainage, impoundment and a general degradation of collecting areas by agriculture, industry and settlements (own observations; see also Dudgeon, 2000, for SE Asia in general), we believe that *S. sulcospira* has become extinct in vast areas on Java. It remains unclear whether and at which localities populations of this species still exist.

Repository Institutions

Voucher material is housed with the following museums: Natural History Museum, London (BMNH), Museum of Comparative Zoology, Cambridge, Mass. (MCZ), Muséum d'Histoire Naturelle, Genève (MHNG), Muséum National d'Histoire Naturelle, Paris (MNHN), Natural History Museum Naturalis, Leiden (RMNH), Senckenbergmuseum, Frankfurt/Main (SMF), Zoölogisch Museum, Amsterdam (ZMA), Museum für Naturkunde, Berlin (ZMB).

We were not able to locate material in the following museum collections: Academy of Natural Sciences, Phil-

adelphia (ANSP), United States National Museum, Washington (UNSM), Zoologisches Institut und Museum, Universität Hamburg (ZMH), Zoologische Staatssammlung, München (ZSM).

Morphological Examinations

Dimensions of all shells were measured to 0.1 mm precision. The shell height (H) is the maximum dimension parallel to the axis of coiling, breadth (B) the maximum dimension perpendicular to H, including the aperture. The length of the aperture (LA) is the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip, the width (WA) the greatest length perpendicular to LA. The height of the body whorl (BW) is the distance from the base of the shell to the upper suture of the first whorl exactly above the junction of the outer lip with the penultimate whorl. Morphometrical parameters used in the analyses, beside the shell dimensions, were: H/B, H/LA, H/BW, H/LA and B/BW. These shell parameters were statistically analyzed by performing t-tests, one-way ANOVA, and a discriminate analysis.

Protoconchs removed from dried adults were cleaned by soaking in 10% KOH solution, flushed in distilled water, and sonicated to remove residual contaminations prior to scanning electron microscopy. Radulae were taken from dried shells or from historic preparations. Radulae from dried shells were enzymatically cleaned as described by Holznagel (1998); an old radula embedded in Canada balsam was cleaned with xylene followed by sonication. Radulae and juvenile shells were mounted on aluminum specimen stubs using adhesive carbon tabs or double-sided tape, respectively, and coated with gold-palladium for 120 s at 20 mA for examination under a scanning electron microscope (LEO 1450 VP) at 10 keV.

Nomenclatorial Remarks

Some species-group names introduced by Troschel (1857–1858) are open to discussion. Bouchet (pers. comm.) argued that the usage of the names Bithyniae, Lithoglyphi, Hydrobiae, Ancyloti, Thiarae, and Pachychili by Troschel (op. cit.) contrasts with the rest of his work (Troschel, 1856–1863), in which he stated the ranks of the categories he used and formed names with endings -idea, -ina, or -acea. Because Troschel stated explicitly that he refrained from allocating these groupings at family rank given the somewhat ambiguous morphological data he was faced with, it was suggested that one should ignore these names (Bouchet, pers. comm.). However, some of these names, such as Bithyniidae, Thiaridae, or Hydrobiidae, have been usually published with Troschel (1857–1858) as author. Unless otherwise stipulated, we prefer to refer to Troschel (1857–1858) as author of these names not only because we regard them as available and valid but also in order to maintain stability in their usage; for a statement to the contrary see Bouchet and Rocroi (submitted).

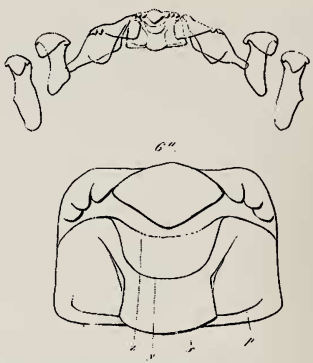


Figure 1. Original drawing of the radula of "*Sulcospira typica* (*Melania sulcospira* Mousson)" by Troschel (1858: pl. 9, fig. 6). In the upper part of the figure a row of teeth is shown comprising a rachidian flanked on each side by a lateral tooth and an inner and outer marginal tooth; a magnified representation of the rachidian is shown below. Characteristics that are typical for Pachychilidae are, e.g., the enlarged main cusp of the rachidian and lateral teeth, respectively, which is flanked by three (or two) smaller cusps on each side that taper in size; the presence and shape of the glabella (or ramp); and marginal teeth possessing two cusps.

Nomenclatorial aspects raised in this paper refer to the stipulations of the 4th edition of the International Code of Zoological Nomenclature ("ICZN") issued by the International Commission of Zoological Nomenclature (1999).

RESULTS

Sulcospira Troschel, 1858

Sulcospira Troschel, 1858: 117–118; Brot, 1874: 56; Thiele, 1929: 190; Morrison, 1954: 381.

Diagnosis: *Sulcospira* possesses a rather conical shell sculptured by spiral lirae; axial sculptural elements are lacking. Protoconchs possess a smooth sculpture with a fine granular texture or faint growth lines.

Type Species: *Melania sulcospira* Mousson, 1849, by monotypy.

Nomenclature and Systematics: The genus *Sulcospira* was described by Troschel (1858) for the Javan species *M. sulcospira* exhibiting certain characteristics that were held to be peculiar of this species, namely a round, multispiral operculum with four regular whorls and the radula with an enlarged main cusp of the rachidian (Figure 1, 17–18). Troschel (1858: 114) based his description on material received from August Brot in Genève, i.e.,

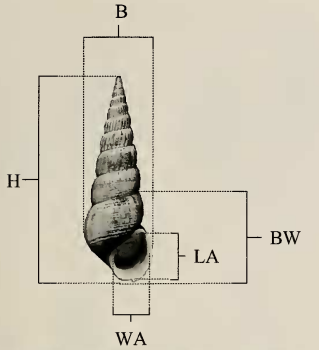


Figure 2. Shell dimensions. B: breadth; BW: weight of the body whorl; H: height; LA: length of the aperture; WA: width of the aperture.

on material that is likely housed at MHNG today (see Material Examined).

Sulcospira represents the oldest available generic name established for representatives of the Southeast Asian Pachychilidae and is here considered valid. However, the diagnosis of Troschel (1858) is not sufficient to characterize the taxon unambiguously. Neither a round and multispiral operculum with four whorls nor the possession of a pronounced main cusp of the rachidian are considered as diagnostic features of *Sulcospira* alone (see discussion). Nonetheless, these features characterize *Sulcospira* as a member of the Pachychilidae (Glaubrecht, 1996, 1999; Köhler and Glaubrecht, 2001, 2002, 2003).

In more recent literature *Sulcospira* has been widely ignored. Thiele (1929) suggested subdividing *Sulcospira* into two subgenera, *Sulcospira* and *Tylomelania* F. and P. Sarasin, 1898. According to Thiele, *Sulcospira* would include *Paracrostoma*, *Acrostoma* Brot, 1870, and *Brotella* Rovereto, 1899, as junior synonyms, consequently comprising two species: *S. sulcospira* from Java and *S. huegeli* (Philippi, 1843) from South India. *Tylomelania*, however, was considered to encompass a small number of species restricted to Sulawesi.

This concept of Thiele (1929) led Subba Rao (1989: 107) to wrongly assume that *M. huegeli* would be the type species of *Sulcospira*, which it is not (see Troschel's original designation).

Later authors had different taxonomic views. Morrison (1954) followed Abbott (1948) but not Thiele (1929) and treated *Acrostoma*, *Brotella*, and *Paracrostoma* as synonyms of *Brotia*, while considering *Tylomelania* as a genus on its own. He also claimed that our understanding of *Sulcospira* is not satisfactory. Based on some superficial similarities with *Brotia*, but also with *Tylomelania* and *Balanocochlis* (a thiarid), Morrison (1954) proposed the allocation of *Sulcospira* "tentatively to the *Melanoides* complex". Since *Melanoides* is a thiarid, this allocation is rejected here.

All these classification schemes were suggested in absence of phylogenetic analyses of morphological characters. In addition to the type species, other taxa have been assigned to the genus by previous authors, although this has not been done consistently (Table 1). The various opinions led also to different assumptions on the species circumscription and diversity of this taxon. For example, Brot (1874) subsumed a number of taxa under *Sulcospira*, of which we currently only consider two to be actually pachychilids: *Melania spadicea* Reeve, 1860, and *M. hainanensis* Brot, 1872. Yen (1939) added two more taxa, *M. ebenina* Brot, 1883, and *M. biconica* Brot, 1886. Boettger (1890), Oostingh (1932), and Adam and Leloup (1838) treated *M. testudinaria* von dem Busch, 1842, as member of *Sulcospira* but did not mention the former taxa. In contrast, other authors assigned those taxa to *Brotia* instead (Rensch, 1934; Benthem-Jutting, 1956, 1959; Knipper, 1958; Dudgeon, 1982, 1989; Köhler and Glaubrecht, 2001, 2002). Eventually, Benthem-Jutting (1956) assumed that *S. sulcospira* is the only representative of the genus.

In order to clarify the puzzling taxonomy and systematics, a revision of *Sulcospira* with an evaluation of its anatomical characters is needed. A sound classification has to be based on autapomorphic features, which is lacking to date. Unfortunately, a comprehensive description of the morphology of *Sulcospira* suffers from the

Table 1. Comparison of previous views on the systematics and circumscription of *Sulcospira*.

	Authors			
	Brot (1874)	Thiele (1929)	Morrison (1954); Benthem-Jutting (1956)	Köhler and Glaubrecht (2002)
Taxonomy at generic level	*Melania* (*Sulcospira*)	*Sulcospira* (*Sulcospira*), *Sulcospira* (*Tylomelania*)	*Sulcospira*	*Sulcospira*
Included taxa	*M. sulcospira*, *M. spadicea*, *M. hainanensis*, and other non-pachychilid taxa	*S. sulcospira*, *S. huegeli*, *T. neritiformis*, *T. carbo*, *T. porcellanica*	*S. sulcospira*	*S. sulcospira*, *S. spadicea*

Table 2. Shell parameters [mm] of *S. sulcospira* and *S. martini*. Abbreviations: B: breadth; BW: weight of the body whorl; H: height; LA: length of the aperture; m: median; N: number of whorls; No: number of shells; sd: standard deviation; WA: width of the aperture.

Lot		No	H	B	LA	WA	BW	N
***S. sulcospira* (total)**	**m**	**26**	**19.3**	**10.1**	**9.5**	**4.9**	**14.3**	**4.7**
	sd		**2.5**	**1.3**	**1.0**	**0.6**	**1.9**	**0.5**
Holotype *M. sulcospira*		1	23.2	12.0	9.7	5.0	15.2	4.0
S. sulcospira (ZMA)	m	21	19.5	10.2	9.5	4.9	14.4	4.6
	sd		2.2	1.2	0.9	0.5	0.6	0.6
S. sulcospira (MNHN)	m	4	18.7	9.9	9.3	4.9	14.1	4.8
	sd		3.6	1.8	1.5	0.9	2.9	0.4
***S. martini* (total)**	**m**	**58**	**27.6**	**12.0**	**11.0**	**5.9**	**17.7**	**6.0**
	sd		**4.5**	**1.5**	**1.3**	**0.8**	**2.1**	**1.0**
Syntypes *M. spadicea* (BMNH 19990497)	m	3	25.5	11.6	10.2	5.2	16.1	6.0
	sd		0.7	0.2	0.9	0.6	0.9	0.5
Syntypes *M. junghuhni* (RMNH, ZMA)	m	22	29.9	12.4	11.6	6.0	18.4	6.3
	sd		4.6	1.8	1.4	0.9	2.4	0.7
Syntypes var. *flammulata*, var. *fasciata* (RMNH)	m	16	28.7	12.3	11.7	6.1	17.9	6.6
	sd		2.9	1.2	1.1	0.7	1.7	0.6
S. martini (ZMB 4.074)	m	17	23.8	11.2	11.0	5.7	16.9	4.9
	sd		2.9	1.3	1.0	0.5	1.7	0.7

lack of well-preserved material of the type species. We compile below the anatomical data based on the material of *S. sulcospira* available.

Sulcospira sulcospira (Mousson, 1849)

Melania sulcospira Mousson, 1849a [1848]: 269; Mousson, 1849b; 68, pl. 9, fig. 3; Martens, 1897: 245 (*partim*); Leschke, 1914: 251.

Sulcospira typica Troschel, 1858: 117, 118, pl. 9, fig. 6 [introduced as replacement name for *M. sulcospira* Mousson, 1849].

Pachycheilus sulcospira [sic].—H. and A. Adams, 1858: 299.

Melania (*Sulcospira*) *sulcospira*.—Brot, 1870: 277; Brot, 1874: 56–57, pl. 6, fig. 11; Boettger, 1890: 245.

Sulcospira sulcospira.—Morrison, 1954: 381; Köhler and Glaubrecht, 2002: 149, fig. 3 L.

Diagnosis: Shell relatively small (Table 2), conical with spiral lirae, and a subsutural depression; aperture elongately ovate, abapically flared. Radula with squarish rachidian exhibiting a straight upper and lower rim, the cutting edge of all teeth with one very pronounced main cusp of triangular shape.

Description: *Shell* (Figures 3–5): small, ovate to conical, solid, spire with eroded apex and up to six flattened whorls, separated by a narrow suture; sculpture consisting of fine, regular spiral lirae that are most prominent at the base and may almost lack on upper whorls, and faint growth lines; whorls with a subsutural depression; color from yellowish to olive or dark brown. Aperture elongately ovate, abapically flared, peristome sharp; columella slightly bent and thickened.

Protoconch (Figures 19–20): Relatively large, compared to the adult; with height of about 1.2 mm comprising one and a half whorl; generally smooth. Apical whorl inflated, dome-shaped, with a granular surface sculpture, transition in sculpture visible on first whorl from granular to faint growth lines. One sample of four specimens housed at MNHN (ex coll. Staat) has a label stating that "about 140 embryos were obtained from the large specimen". However, the fate of these protoconchs is unknown.

Operculum: With four whorls regularly increasing in diameter and a sub-central nucleus.

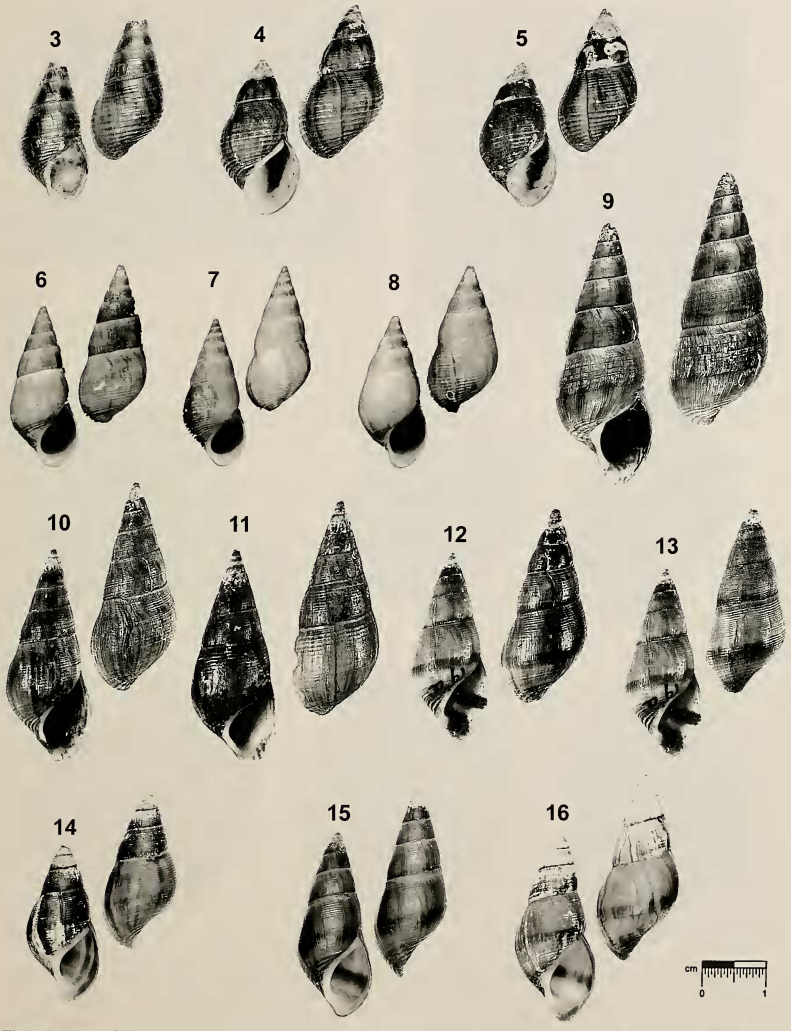
Radula (Figures 16–17): Rachidian tooth squarish with a straight upper and lower rim, cutting edge with one heavily enlarged main cusp of triangular shape, flanked by two, much smaller accessory cusps on each side; glabella well developed, rather rectangular with a rounded basal margin not exceeding the lower rim of the rachidian tooth, lateral margins straight and not well defined. Lateral teeth with one heavily enlarged main cusp, and considerably smaller accessory cusps, one at the outer side, two or three at the inner side. Inner and outer marginal teeth with two cusps, the outer one being very large, triangular in shape, and the inner one being pointed and small. Inner marginal teeth broader than outer marginals. Outer lateral flange inconspicuous.

Anatomy: Unknown.

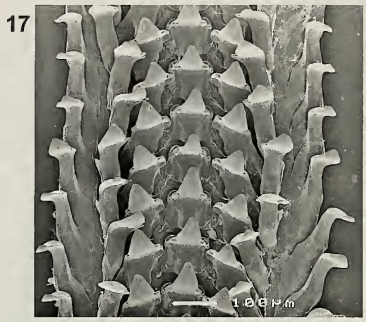
Type Material: Indonesia: Holotype ZMZ 522306, Indonesia: Java, leg. Zollinger (Figure 3) [Mousson, 1849b refers to "das einzige Exemplar dieser Art . . ." = the only specimen of this species . . .].

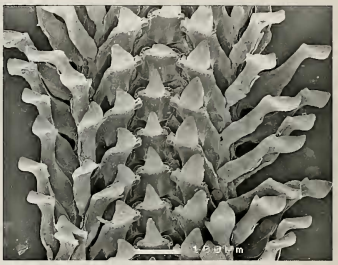
Type Locality: "Java", Indonesia.

Other Material Examined: Indonesia: Java (MHNG; MNHN; MNHN, ex coll. Staat; ZMA (2 lots); ZMB 200.101) (if not stated otherwise, a single lot from each collection, mostly without reference number, was examined); museums without material: ANSP, BMNH, MCZ, RMNH, SMF, USNM, ZMH, ZSM.



Figures 3–16. Shell morphology of *Sulcospira sulcospira* (**3–5**) and *S. martini* (**6–16**) (apertural and abapertural, respectively). **3.** *S. sulcospira.* Holotype (ZMZ 522306). **4–5.** *S. martini.* Two shells from Java (ZMA). **6.** Lectotype of *M. spadicea* (BMNH 19990497/A). **7–8.** Two paralectotypes of *M. spadicea* (BMNH 19990497/B). **9.** Lectotype of *M. junghuhni* (RMNH 71326). **10–11.** Two syntypes of *M. junghuhni* var. *flammulata* (RMNH 71327). **12–13.** Two syntypes of *M. junghuhni* var. *fasciata* (RMNH 71328). **14–16.** Three shells from Java, Malangbong (ZMB 4.074). Scale bar = 10 mm.





Figures 17–24. SEM images of the radula and juvenile shells removed from dry shells of *S. sulcospira* (**17–20**) and *S. martini* (**21–24**). *S. sulcospira*: **17.** Radula (ZMA). **18.** Radula (ZMB 200.101). **19.** Juvenile shell, apertural view (ZMA). *S. martini*: **20.** Juvenile shell, apical view (ZMA). **21.** Juvenile shell, apertural view (ZMB 4.074). **22–23.** Apical view. **24.** Detail of the apical portion. Scale bars = 100 μm.

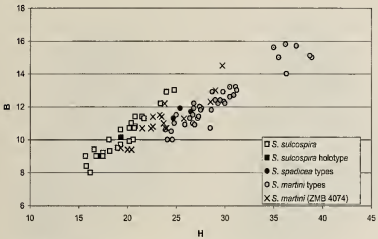


Figure 25. Comparison of the shells of *S. sulcospira* and *S. martini* based on shell parameters height (H) and breadth (B).

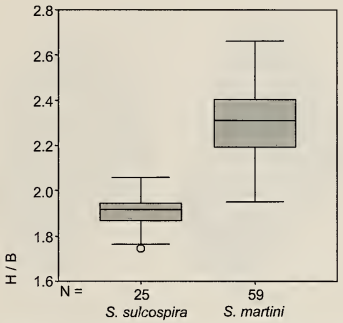


Figure 26. Comparison of *S. sulcospira* and *S. martini* based on shell parameters ratio H/B. Box plot diagram showing the median, the 25%- and 75%-percentile and largest non-extremes (less than 1.5 times of box height).

Distribution: Indonesia: Java. More precise localities were given by Boettger (1890: Bogor Botanical Garden) and Martens (1997: Jakarta, Malangbong, Cipanas). However, the material of Boettger could not be traced (SMF?), and Martens misidentified material of *Melanoides tuberculata* (Cipanas) and *S. martini* (Malangbong; ZMB 4.076); no voucher material was found from Jakarta.

Nomenclature and Systematics: *Melania sulcospira* is the type species of the genus *Sulcospira* by original designation. When describing the new genus, Troschel (1858), mentioned *M. sulcospira* as the "typical species", and introduced the name *S. typica* for the same taxon as a new, unnecessary substitute name meant to replace an older available name (*nomen novum*). Thus, *S. typica* is a junior synonym of *S. sulcospira* (ICZN Art. 72.7.). *Sulcospira typica* is invalidated as potential type name (ICZN Art. 68.4.) making *M. sulcospira* the type by absolute autonomy. Martens (1897) assumed that *M. spadicea* is a synonym of this species, which was rejected by Leschke (1914) and Benthem-Jutting (1956: 373), stating that Martens (1897) had misidentified specimens of *Melanoides tuberculata* for *M. spadicea.*

Remarks: Compared to *Sulcospira martini, S. sulcospira* is more conical in shape; the former lacks a conspicuous subsutural depression. Most conspicuously, both species differ in their protoconch morphology. Shells of *B. testudinaria* are more elongated in shape, attain a larger size (between 25 to 40 mm in shell height), lack a subsutural depression, and exhibit a different radular morphology: e.g., rachidian with inflated and rounded upper corners, a smaller main cusp, marginal teeth possess two equally shaped cusps.

Given the scarcity of material and imprecise earlier locality data for this material, we tried to restrict the type locality from historical accounts. The Swiss malacologist Albert Mousson (1805–1890) based his descriptions on material collected by the Swiss botanist Heinrich Zollinger (1818–1859), who traveled in Indonesia between 1842 and 1848. However, as Zollinger collected not only in West Java, but later also in East Java, and on some other islands (Wanner, 1984), it turned out that a restriction of the type locality is not possible and "Java" remains as the only known reference.

Sulcospira(?) *martini* (Schepmann, 1898)

Melania spadicea Reeve, 1860: pl. 19, species 132 (not *Melania spadicea* Philippi, 1849); Brot, 1870: 277.

Melania (*Sulcospira*) *spadicea.*—Brot, 1874: 57–58, pl. 6, fig. 12.

Brotia spadicea.—Benthem-Jutting, 1956: 372–373, fig. 75.

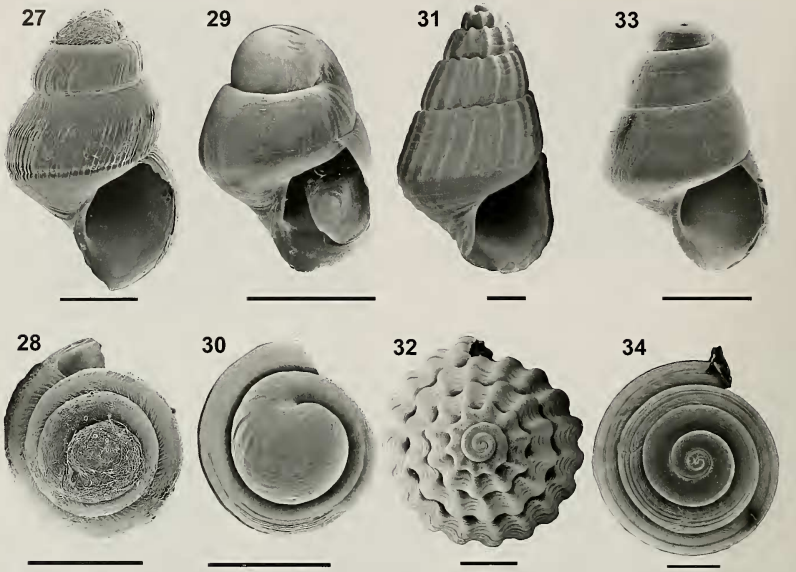
Sulcospira spadicea.—Köhler and Glaubrecht, 2002: 148, fig. 3G.

Melania junghuhni Schepman, 1896: 135–136, pl. 2, fig. 1. ("Java"; lectotype and 41 paralectotypes RMNH 71326; 24 paralectotypes ZMA; two paralectotypes SMF 292406; var. *flammulata*: 16 syntypes RMNH 71327; 3 syntypes MCZ 96926, var. *fasciata*: 18 syntypes RMNH 71328; 24 syntypes ZMA; 8 syntypes MCZ 96898) (not *M. junghuhni* Martin, 1879); Leschke, 1914: 251; Benthem-Jutting, 1929: 84.

Melania martini Schepmann, 1898: 84.

Brotia testudinaria.—Köhler and Glaubrecht, 2001: 301–304 (*partim*); Köhler and Glaubrecht, 2002: 140, 141, 150 (partim).

Diagnosis: Conical shell with convex to flattened whorls sculptured with fine spiral ridges. Protoconch with about 2.5 regular whorls; apical whorl not inflated, no transition in shell structure is visible in the first two whorls. Axial ribs may be present in the juvenile shell from the second whorl on. Most conspicuously distinguished from all other pachychilids by its protoconch morphology (Figures 27–34); distinguishable from *S. sulcospira* by its more elongated and larger shell (Figure 26); though adult shell not distinguishable from *B. testudinaria.*



Figures 27–34. Comparison of protoconchs of different southeastern Asian Pachychilidae (apertural and apical view, respectively). **27–28.** *Brotia costula.* **29–30.** *Brotia hainanensis.* **31–32.** *Tylomelania patriarchalis* (with kind permission of Thomas von Rintelen). **33–34.** *Pseudopotamis semoni.* Scale bars = 100 μm.

Description: *Shell* (Figures 6–16): Small to medium sized (Table 2), ovate to conical, spire with eroded apex and eight to ten flattened whorls; sculpture consisting of fine, closely spaced regular spiral lirae, may lack almost completely, and faint growth lines; color yellowish brown to olive, brown spiral band or patches may be present. Aperture elongated ovate, produced below, peristome sharp.

Protoconch (Figures 21–24): Height of about 1.2 mm comprising 2½ whorls; apical whorl not inflated, corresponding to the regular diameter of the subsequent whorls; first two whorls smooth, only faint growth lines visible, without transition in sculpture, from the second whorl on smooth axial ribs may be present.

Operculum: Consisting of three whorls and a sub-basal nucleus Brot (1874).

Anatomy and Radula: Unknown.

Type Material: Indonesia, Java: Lectotype and 41 paralectotypes of *M. junghuhni*, RMNH 71326, leg. Junghuhn (Figure 9), designated by Köhler and Glaubrecht (2002); 24 paralectotypes, ZMA; two paralectotypes, SMF 292406; 16 syntypes of *M. junghuhni* var. *flammulata*, RMNH 71327; three syntypes, MCZ 96926, 18 syntypes of *M. junghuhni* var. *fasciata*, RMNH 71328; eight syntypes, MCZ 96898. Without locality: Lectotype of *M. spadicea*, BMNH 19990497/A, Cuming collection, designated by Köhler and Glaubrecht (2002); two paralectotypes, BMNH 19990497/2.

Type Locality: "Java", Indonesia.

Other Material Examined: Without locality (ZMA; MHNG); Indonesia: Java (MHNG), Malangbon (ZMB 4.074) (a single lot from each collection, mostly without reference number). No material was found in the following museums: ANSP, MNHN, SMF, USNM, ZMH, ZSM.

Nomenclature and Systematics: *Melania spadicea* Reeve, 1860, is a primary homonym of *M. spadicea* Philippi, 1849 (ICZN Art. 53.3) and, as such, is permanently invalid (ICZN Art. 57.2). The next available names are *M. junghuhni* Schepmann, 1896, *M. junghuhni* var. *flam-*

mulata Schepmann, 1896, and *M. junghulni* var. *fasciata* Schepmann, 1896. However, the first is a primary homonym of *Melania junghuhni* Martin, 1879, a fossil species from Java, as stated by Schepmann (1898). The other two are junior primary synonyms of *Melania flammulata* von dem Busch in Philippi, 1843, and *Melania fasciata* Menke, 1828, respectively.

Schepmann (1898) suggested *Melania martini* as a replacement name for *M. junghuhni*, which is the valid name for this taxon. The two color morphs described by Schepmann (1896), *fasciata* and *flammulata*, are not considered here to represent extant evolutionary entities and therefore are treated as junior synonyms of *M. martini*.

The classification of this species by former authors is inconsistent. Benthem-Jutting (1956) considered it to be a member of *Brotia*; but unaware of the fact that *M. spadicea* Reeve, 1860, is not valid she assumed that this name had priority over *M. martini*. Köhler and Glaubrecht (2002) assumed that *M. martini* and *M. spadicea* are distinct and treated the former as a synonym of *B. testudinaria* and the latter as a species closely related to *S. sulcospira* as was suggested earlier by Brot (1874).

Distribution: Java, as the only known locality. Malangbon in Central Java, east of Bandung, is the only known exact locality (ZMB 4.074, catalogued in 1859).

Analyses of Shell Morphometry: *Sulcospira martini* can be distinguished from *S. sulcospira* by its higher shell and more slender shape (see analyses of shell parameters below). However, to differentiate between shells of "*M. sulcospira*" and "*M. martini*" is no easy task; contradictory statements on their taxonomy abound in earlier accounts (Brot, 1874; Benthem-Jutting, 1956; Köhler and Glaubrecht, 2002). In fact, shells exhibit a very similar shape, sculpture, and coloration. However, the two taxa can be distinguished by statistical analyses of shell morphometry. We used one-way ANOVA and t-test for two independent groups of variables to discriminate specimens that were assigned beforehand either to *S. sulcospira* or to *S. martini* according to their shell morphology. The t-test showed that both taxa vary significantly by the following parameters (P<5%): H, N, H/B, H/LA, and H/BW; the one-way-ANOVA yielded corresponding results.

The shells of the only lot from Java with precise locality data (ZMB 4.074) is identified here as *S. martini* given its elongated shell (while the original label states "*M. sulcospira*" instead). The statistical test has been employed to explore whether these shells can significantly be discriminated either from shells of *S. sulcospira* or *S. martini* in regard to shell morphometry. Comparison of shells of the lot ZMB 4.074 with shells of *S. sulcospira* (MNHN, ZMA, ZMB 200.101, ZMZ 522306) by t-test reveals that both groups differ significantly in the parameters H/LA, H/BW, and with a weak support (P = 0.51) for H/B, whereas no significant differences were found when comparing the lot ZMB 4.074 with other shells of *S. martini* (BMNH 19990497, RMNH 71326-8).

Table 3. Results of the discriminate analysis of shell parameters.

Predicted group membership	*S. sulcospira*	*S. martini*
S. sulcospira	25 (100.0%)	0 (0.0%)
S. martini	1 (1.7%)	59 (98.3%)

A graphic comparison of the two taxa by means of selected shell parameters is shown in Figures 25–26. Shells assigned to each of the two taxa according to their morphology were found to be correctly classified by a discriminate analysis of morphometric data with good statistical support (Table 3). It is concluded that shells of *S. sulcospira* are smaller and more conical in shape than shells of *S. martini* (Table 1, Figure 26).

DISCUSSION

1. Evaluation of Morphological Characters of *Sulcospira*

The operculum and radula of *S. sulcospira* led Troschel (1858) to describe a new genus for this species. However, among the Pachychilidae the operculum is known to be relatively conservative in its general organization (that is, to be multispiral, rounded or ovate) but quite variable in relation to their number of whorls and increase in diameter, even within a single genus (Köhler and Glaubrecht, 2001, for *Brotia*; Köhler and Glaubrecht, 2003, for *Jagora*; Glaubrecht and Rintelen, 2003, for *Pseudopotamis*; Rintelen, 2003, for *Tylomelania*; Köhler, 2003). Consequently, an operculum possessing four regular whorls might be typical for *S. sulcospira*, but only at the species level. The possession of a round to oval, multispiral operculum led Sarasin and Sarasin (1898) to group several taxa within the so-called "palaeomelanians", as contrasted with the so-called "neomelanians", which exhibit a paucispiral operculum. In fact, this grouping coincides well with the modern concept of the Pachychilidae and Thiaridae, respectively (Glaubrecht, 1996, 1999; Köhler and Glaubrecht, 2001, 2002, 2003). Therefore, operculum morphology in *S. sulcospira* corroborates the placement of the taxon within the Pachychilidae. This, however, represents a plesiomorphic character state among the representatives of this family, and is not a suitable character to establish generic distinction.

By and large, the same can be stated for the radula. The molluscan radula is generally considered a conservative character (Fretter and Graham, 1994). The pattern described and depicted by Troschel (1858) (Figure 1) is commonly found among pachychilids (Köhler and Glaubrecht, 2001, 2002, 2003; Glaubrecht and Rintelen, 2003; Rintelen and Glaubrecht, 1999, 2003). This had been already noticed by Troschel (1858), when allocating taxa such as *Pachychilus* and *Sulcospira* (but also *Me-*

lanopsis) under the "Pachychili". However, we have been unable to identify a single radular character peculiar to *Sulcospira*, based on the limited anatomical features discussed here. An enlarged main cusp is also found in other pachychilid species, such as *B. pagodula* (Köhler and Glaubrecht, 2001). Moreover, it is evident that radular characters may especially be prone to adaptation, parallelism, and convergence and that intraspecific variability and plasticity in general may be considerable, as described, e.g., for littorinid gastropods (Padilla, 1998; Reid and Mak, 1999; Reid, 2000). Thus, possession of an elongated cusp alone is not considered a characteristic suitable for the diagnosis of *Sulcospira*.

Gross anatomy of *S. sulcospira* and *S. martini* remains unknown, due to the lack of ethanol-preserved specimens. It has been shown for other pachychilids, though, that particularly characters of the reproductive organs (pallial oviduct, gonads, brooding structures) and the protoconch may bear essential systematic information (Köhler and Glaubrecht, 2001, 2003).

Juvenile shells extracted from dried adults (Troschel, 1858; and own observations) deliver circumstantial evidence that *Sulcospira* is viviparous. Furthermore, as made evident from the following comparison, the protoconchs of *S. sulcospira* are similar to those of some species we have primarily assigned to the "*Brotia-testudinaria*-group" (Köhler and Glaubrecht, 2001, e.g., *Brotia testudinaria* and *B. hainanensis*; Figures 29–30). In contrast, other taxa constituting the genus *Brotia* sensu stricto (denominated the "*Brotia pagodula* group" by Köhler and Glaubrecht, 2001) have juveniles with an irregularly wrinkled sculpture of the apical whorl of the protoconch (Figures 25–26). Protoconchs of *Tylomelania* and *Pseudopotamis* exhibit yet another fine morphology (Figures 27–34). They attain a relative large size and exhibit a relatively small apical whorl with a smooth shell as well as regularly increasing whorls (Rintelen and Glaubrecht, 1999, 2003; Glaubrecht and Rintelen, 2003).

As discussed in some detail by Köhler and Glaubrecht (2001), distinct protoconch morphologies of several pachychilid genera are correlated with different reproductive strategies. For example, *Brotia* possesses a subhaemocoelic brood pouch while representatives of *Tylomelania* and *Pseudopotamis* are characterized by an eu-viviparous mode of reproduction utilizing a modified oviduct as brood pouch (= uterine brood pouch; Rintelen and Glaubrecht, 1999; Glaubrecht and Rintelen, 2003). Females of the latter two taxa retain a small number of embryos in the uterus that are nourished by secretions produced by the albumen gland.

The protoconchs of *Sulcospira* correspond to those of the so-called "*Brotia testudinaria* group" (Köhler and Glaubrecht, 2001), which indicates to us that *S. sulcospira* possesses a subhaemocoelic brood pouch as well.

II. Comparison of *S. sulcospira* and *S. martini*

Sulcospira martini, which has tentatively been allocated to the genus by Köhler and Glaubrecht (2002), can be distinguished by its shell, but much more conspicuously by its different protoconch morphology, which is unique among the Pachychilidae.

Because the protoconch morphology is related to the mode of reproduction, it is assumed that *S. martini* exhibits reproductive features (e.g. incubatory structure, reproductive strategy) that may be distinct from those known from any other pachychilid taxon.

III. Systematic Conclusions

Shell, operculum, and radula of *S. sulcospira* (and also of *S. martini*) are typically pachychilid; a basally well rounded and flared aperture, a round to oval, multispiral operculum, and a rachidian tooth with an enlarged main cusp flanked by up to three accessory cusps that taper in size are diagnostic characters of this family. However, these characters are symplesiomorphic and, thus, uninformative at the generic level. Soft body morphology, which could bear crucial information, is not known. Still, some systematic conclusions can be drawn based on the evaluation of protoconch morphology, which is considered to be more or less constant at the generic level: First, species of *Brotia* (Figures 27–28), *Tylomelania* (Figures 31–32), and *Pseudopotamis* (Figures 33–34) are not congeneric with *S. sulcospira* (see Figures 19–20) since they exhibit each a distinct protoconch, which is testimony to a different reproductive strategy as discussed above. The same holds true for *Jagora* (Köhler and Glaubrecht, 2003). All these pachychilid genera have been shown to represent independent monophyletic lineages characterized by morphological features, such as peculiar reproductive morphologies. Second, the protoconch of *S. sulcospira* is very similar to that known from species of the "*Brotia-testudinaria*-group" denominated by Köhler and Glaubrecht (2001) (Figures 29, 30 for *B. hainanensis*). Hence, *Sulcospira* Troschel, 1858, being available and valid, might be an appropriate generic name for this species group under the precondition that it can be shown that a protoconch with a smooth and dome-shaped apical whorl is a character possessed by the members of this group and derived by shared ancestry. However, the alternative explanation that a similar protoconch represents an ancestral state that is present in two different lineages has to be ruled out. Otherwise, inferring generic relationship in absence of a phylogenetic evaluation could lead to the erection of paraphyletic taxa when the characters considered are plesiomorphic. Before we cannot show by phylogenetic analyses of morphological or molecular data that *S. sulcospira* and species of the "*Brotia testudinaria* group" indeed belong to the same taxon, we therefore refrain from a respective taxonomic suggestion.

Third, we conclude that *S. martini* can be recognized as a species and that it does not represent a synonym of *S. sulcospira*. Furthermore, it is clear that the morphology of the protoconch of *S. martini* does resemble neither of the known pachychilid genera very closely (Figures 27–34) including that of *S. sulcospira* (Figures 19–

20). Just based on this single feature, it could be deduced that *S. martini* might be a representative of a yet undescribed genus. However, as has been stated for *S. sulcospira*, a sound decision on its systematics should rely on a more comprehensive data set.

For the time being, we suggest to maintain *Sulcospira* as a monotypic genus endemic to Java. Furthermore, we refrain from a taxonomic decision on the generic relationship of "*Sulcospira*" *martini*. It likely is not a member of one of the described pachychilid genera, but its true relationships remain unknown.

Irrespective of our anticipation that both species dealt with in this paper may have already become extinct in large parts of their original distribution area, we still hope that suitable material will turn up, eventually allowing to find an answer to the remaining questions and to solve another of the many puzzling aspects of pachychilid phylogeny and systematics that long hampered a deeper understanding of the evolution of this intriguing and instructive case study among the lymnic Cerithioidea.

ACKNOWLEDGMENTS

We are most grateful to the curators Philippe Bouchet (MNHN), Yves Finet (MNHG), Edmund Gittenberger and Jeroen Goud (RMNH), Ronald Janssen (SMF), Trudi Meier (ZMZ), Robert Moolenbeek (ZMA) and Kathie Way (BMNH) for making material of their collections available to us. Thomas von Rintelen kindly provided SEM images of a juvenile shell of *Tylomelania patriarchalis*. We thank Philippe Bouchet and an anonymous reviewer for most helpful comments on the manuscript, in particular as related to nomenclatorial aspects. Their comments helped much to improve the quality of this paper. The work of F. K. was funded through a postgraduate scholarship of the Konrad-Adenauer-Stiftung, Sankt Augustin (Germany). This paper is part of a project on Southeast Asian pachychilids supported through grant GL 297/4 to M.G. by the Deutsche Forschungsgemeinschaft.

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